Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking

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Abstract

Walking is a motor task requiring coordination of many muscles. Previous biomechanical studies, based primarily on analyses of the net ankle moment during stance, have concluded different functional roles for the plantar flexors. We hypothesize that some of the disparities in interpretation arise because of the effects of the uniarticular and biarticular muscles that comprise the plantar flexor group have not been separated. Furthermore, we believe that an accurate determination of muscle function requires quantification of the contributions of individual plantar flexor muscles to the energetics of individual body segments. In this study, we examined the individual contributions of the ankle plantar flexors (gastrocnemius (GAS); soleus (SOL)) to the body segment energetics using a musculoskeletal model and optimization framework to generate a forward dynamics simulation of normal walking at 1.5 m/s. At any instant in the gait cycle, the contribution of a muscle to support and forward progression was defined by its contribution to trunk vertical and horizontal acceleration, respectively, and its contribution to swing initiation by the mechanical energy it delivers to the leg in pre-swing (i.e., double-leg stance prior to toe-off). GAS and SOL were both found to provide trunk support during single-leg stance and pre-swing. In early single-leg stance, undergoing eccentric and isometric activity, they accelerate the trunk vertically but decelerate forward trunk progression. In mid single-leg stance, while isometric, GAS delivers energy to the leg while SOL decelerates it, and SOL delivers energy to the trunk while GAS decelerates it. In late single-leg stance through pre-swing, though GAS and SOL both undergo concentric activity and accelerate the trunk forward while decelerating the downward motion of the trunk (i.e., providing forward progression and support), they execute different energetic functions. The energy produced from SOL accelerates the trunk forward, whereas GAS delivers almost all its energy to accelerate the leg to initiate swing. Although GAS and SOL maintain or accelerate forward motion in mid single-leg stance through pre-swing, other muscles acting at the beginning of stance contribute comparably to forward progression. In summary, throughout single-leg stance both SOL and GAS provide vertical support, in mid single-leg stance SOL and GAS have opposite energetic effects on the leg and trunk to ensure support and forward progression of both the leg and trunk, and in pre-swing only GAS contributes to swing initiation. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Studies have identified strong correlations between the net ankle moment and power produced by the ankle plantar flexors and gait performance in several patient populations (Mueller et al., 1995; Nadeau et al., 1999; Olney et al., 1990; Olney et al., 1994; Winter et al., 1990). Nevertheless, the functional role of the ankle

muscles during gait (normal and pathological) has remained controversial. Previous experimental (e.g. Winter, 1991; Perry, 1992) and theoretical (e.g. Kepple et al., 1997; Riley and Kerrigan, 1999) studies have been limited to assessing the functional role of the ankle plantar flexors as a single unit because the analyses were based on the net ankle joint moment derived from inverse dynamics. Biomechanical analyses based on net ankle (and knee) joint moments cannot elucidate the potentially different mechanical contributions of individual uniarticular and biarticular plantar flexor muscles to the overall gait performance (e.g. support and

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forward progression). We believe that the lack of consensus regarding the functional roles of the plantar flexor muscles results in part because of the difficulty in rigorously quantifying a muscle's contribution to the individual body segment energetics (i.e. acceleration and power) and in part because individual muscles within the plantar flexor group likely contribute to the body segment energetics differently.

The three main theories advanced in the literature have been that the ankle plantar flexor group: (1) provide a controlled roll-off (e.g. Sutherland et al., 1980; Perry, 1992), (2) actively provide forward progression or push-off (e.g. Winter, 1983; Kepple et al., 1997) and (3) accelerate the leg into swing (e.g. Hof et al., 1993; Meinders et al., 1998). These theories are not likely to be mutually exclusive, as the plantar flexor group may contribute to each of the proposed functions, either by individual plantar flexor muscles performing the different functions or by synergistic actions between them.

The controlled roll-off theory describes forward progression during single-leg stance as a controlled fall (Perry, 1992). Thus, the proposed primary action of the ankle plantar flexors during the controlled roll-off is to decelerate tibia rotation and prevent knee flexion as the body rotates over the stance leg. Forward progression is then the result of a passive mechanism as the body moves forward as a result of momentum and inertia. Supporting evidence for the controlled roll-off theory is found in a pair of clinical studies using tibial-nerve blocks to temporarily paralyze the plantar flexors (Simon et al., 1978; Sutherland et al., 1980). Both studies found that in the absence of normal plantar flexor activity, walking velocity increased, leading them to conclude that the plantar flexors restrain forward momentum rather than propel the body forward. However, during both studies, walking mechanics (e.g. step length, step time, joint angles) were altered by the nerve blocks, making comparisons with unaltered plantar flexor function difficult.

The active push-off theory hypothesizes that the energy generated by the plantar flexor group is transferred to the trunk to provide support and forward progression. Winter (1983) examined the power output of the net ankle and knee joint moments during normal gait and found that the ankle moment was the primary source of positive work, and that plantar flexor activity coincided with the second peak of the vertical ground reaction force. He concluded that an active plantar flexor push-off, rather than a passive roll-off, provides forward progression. Supporting evidence was provided in a recent theoretical study that showed the plantar flexor moment was the primary contributor to the accelerations of the head–arms–trunk segment in both the horizontal (considered analogous to forward progression) and vertical (considered analogous to support)

directions during the second-half of the single-leg stance phase (Kepple et al. 1997).

The final theory suggests that the primary function of the ankle plantar flexors is to accelerate the leg into swing, and forward progression is provided later in the swing phase as energy from the swing leg is transferred to the trunk (Hof et al., 1993, Meinders et al., 1998). Meinders et al. (1998) performed inverse dynamics and mechanical energy analyses to show that, although the net ankle moment generated the majority of the mechanical work during the push-off phase, only a small portion of this mechanical energy was transmitted to the trunk segment. Instead, their data showed that the mechanical work generated by the net ankle moment was stored in the swing leg as kinetic and potential energy. Similarly, Hof et al. (1993) examined correlations between changes in body segment mechanical energy and work of the triceps surae group determined from electromyogram to force processing and concluded that the primary function of the ankle plantar flexors is to provide the energy necessary for swing leg initiation.

The three different theories for the role of the plantar flexors in gait may not, however, be mutually exclusive since the uniarticular plantar flexors (e.g., soleus) and biarticular plantar flexors (e.g., gastrocnemii) individually or working in synergy may contribute to each of the proposed theories above. However, net joint torque-based analyses, as used in the studies proposing these theories, cannot differentiate between the contributions of the uniarticular and biarticular plantar flexors to task performance and, therefore, cannot identify their functional roles.

To date, no study has quantified the contributions of *individual* plantar flexor muscles to the acceleration of (and power delivery to) the individual body segments during walking, which are crucial to understanding the distinct roles of the uniarticular and biarticular plantar flexors. Previous studies have suggested functional roles for individual muscles based on correlational-type analyses (e.g., correlation of EMG activity with kinematics and kinetics, Pedotti, 1977; Winter, 1991; Perry, 1992). However, a muscle force causes significant reaction forces throughout the body, which are either ignored in such analyses or, at best, recognized but provide no solution for calculating them. Similarly, solving the force-sharing problem alone (e.g. Anderson and Pandy, 2001), like inverse dynamics-based analyses, does not provide insight into causal relationships between muscle activity and task performance. But, acceleration and power analyses (Fregly and Zajac, 1996) of forward dynamics simulations of walking, that are driven by individual muscles, can identify how each muscle contributes to the acceleration and power of the leg segments and the trunk to affirm or refute the above three theories.

Therefore, the objective of this study was to use a forward dynamics based analysis to identify how the individual uniarticular and biarticular plantar flexors contribute to support, forward progression and swing initiation. We considered a muscle to contribute to *forward progression* if it accelerated the trunk forward (Kepple et al., 1997), *support* if it accelerated the trunk vertically (Kepple et al., 1997), and *swing initiation* if it contributed positive power directly to the leg segments in pre-swing (Hof et al., 1993). By definition, the controlled roll-off theory implies that muscles do not contribute directly to forward progression.

2. Methods

A forward dynamics simulation of walking driven by individual muscle actuators was developed. This consisted of modeling the musculoskeletal system, muscle force generation and ground contact forces, identifying appropriate initial conditions (positions and orientations of the body segments at heel-strike) and finding the muscle excitations that replicate walking kinematics and kinetics.

2.1. Musculoskeletal model

A forward dynamics musculoskeletal model was developed using SIMM (MusculoGraphics, Inc., Evanston, IL) and consisted of rigid segments representing the trunk, right and left legs. Each leg consisted of a thigh, shank, patella and foot (Fig. 1). The trunk segment included the mass and inertial characteristics of the pelvis, torso, head and arms. The model was dimensioned to represent a male subject with a height of 180 cm and a mass of 75 kg. Musculoskeletal geometry was based on Delp et al. (1990) and segment masses and

inertial properties were determined using regression equations (Clauser et al., 1969; Chandler et al., 1975).

The trunk was allowed to translate and rotate in the sagittal plane. The hip and ankle joints were modeled as frictionless revolutes. The tibiofemoral joint was modeled with a moving center-of-rotation for flexion-extension specified as functions of knee flexion angle (Delp et al., 1990). Passive torques were applied at the hip, knee and ankle joints based on Davy and Audu (1987) to model the forces applied by ligaments and joint structure. The patella was constrained to move along a prescribed trajectory relative to the femur as a function of knee flexion angle (Delp et al., 1990). The model had a total of nine degrees of freedom.

The dynamical equations-of-motion for the model were derived using SD/FAST (Symbolic Dynamics, Inc., Mountain View, CA) and a forward dynamics simulation was produced by Dynamics Pipeline (Musculo-Graphics, Inc., Evanston, IL). The model was driven by 15 individual Hill-type musculotendon actuators for each leg that were combined into nine muscle groups, with muscles within each group receiving the same excitation signal. The muscle groups were defined as PSOAS (iliacus, psoas), GMAX (gluteus maximus, adductor magnus), VAS (3-component vastus), HAMS (medial hamstrings, biceps femoris long head), SOL (soleus), BFsh (biceps femoris short head), GAS (medial and lateral gastrocnemius), RF (rectus femoris) and TA (tibialis anterior). The contraction dynamics were governed by a Hill-type model formulation (Schutte et al., 1993) and the activation dynamics were modeled by a first-order differential equation (Raasch et al., 1997), with activation and deactivation time constants of 50 and 65 ms, respectively.

Excitation of each muscle was modeled as a block pattern defined by onset, duration and one magnitude, except for SOL and GAS which were modeled with additional magnitude levels within the burst duration to
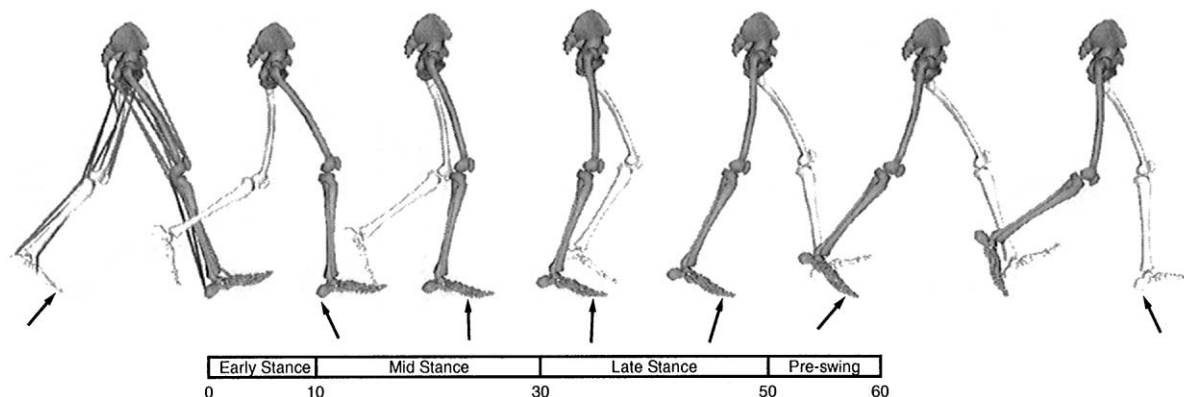

Fig. 1. Gait pattern of the two-legged musculoskeletal walking simulation. The simulation starts and ends with right heel-strike. The model was limited to the sagittal plane and driven by 15 muscle actuators per leg. The average walking speed was 1.5 m/s. Gait cycle duration was 1.1 s. Regions of the stance phase are indicated in percent of the gait cycle. Heel-strike and toe-off occur at 0% and 60% of the gait cycle, respectively. Early stance and pre-swing correspond to approximately double-leg stance.

allow for the characteristic increasing excitation pattern (e.g. Perry, 1992; Winter, 1991). The left and right legs were considered symmetric and 50% of the gait cycle out-of-phase.

2.2. Ground contact model

The contact between the foot and the ground was modeled by 30 independent visco-elastic elements with coulomb friction, each attached to the foot segment in locations that describe the exterior surface of a shoe. Each element permitted deformation perpendicular to the floor and represented the mechanical properties of the shoe sole and underlying soft tissue. The anterior–posterior and vertical force calculations as well as the determination of shoe specific parameters are presented in detail in Neptune et al. (2000b).

2.3. Optimization framework

A simulation of a complete gait cycle (right heel-strike to right heel-strike) that replicated experimental data the best was generated by solving the optimal tracking problem (e.g. Neptune and Hull, 1998; Piazza and Delp, 1996). Using a simulated annealing optimization algorithm, muscle excitation patterns served as the control variables and were systematically varied until the difference between simulated and experimental kinetic and kinematic quantities was minimized (Eq. (1), Neptune, 1999). Muscle excitation magnitudes were constrained to the interval between 0 and 1 (maximally stimulated) and muscle timing to $\pm 25\%$ of the gait-cycle timing presented in Perry (1992), with the exception that RF was allowed to have a second burst of activity during early single-leg stance (e.g. Winter, 1991). The objective function used in the optimization was of the following form:

$$J = \sum_{j=1}^{m} \sum_{i=1}^{n} \frac{(Y_{ij} - \hat{Y}_{ij})^2}{SD_j^2}, \tag{1}$$

where Y_{ij} = measurement of variable j at time step i, $\hat{Y}_{ij}$ = simulation data corresponding to Y_{ij}, SD_j^2 = average inter-trial variability of variable j.

The specific quantities evaluated in Eq. (1) were the right and left hip, knee and ankle joint angles, net joint moments and powers, horizontal and vertical ground reaction forces, and the two components (x, y) of the trunk translation resulting in a total of $m = 22$ variables in the objective function Eq. (1). The optimization was terminated when the objective function decreased by $\leqslant 1\%$ within 500 function evaluations.

2.4. Experimental data

To provide the initial conditions for all the simulations (positions and orientations of the body segments at heel strike) and the experimental quantities in Eq. (1), experimental data were collected at the Rush-Presbyterian-St. Luke's Medical Center (Chicago, IL) from five healthy males (height = 177.0 ± 10.4 cm; weight = 73.3 ± 12.0 kg, age = 22.2 ± 2.1 years) during normal walking. The subjects walked at their self-selected pace while kinematic and ground reaction force data were collected. The average walking speed of all five subjects was 1.5 ± 0.2 m/s. Total stride time was 1.1 s. Intersegmental joint moments were computed using a standard inverse dynamics approach and the joint powers were computed as the product of the corresponding joint moment and angular velocity. A single trial from each subject was processed and averaged across subjects. Details about the data collection and processing can be found in Andriacchi et al. (1997).

2.5. Initial conditions

The initial kinematic conditions for each simulation in the optimization search were obtained through measurement and optimization. The initial trunk position and leg segment orientations were obtained from the average subject experimental data at touchdown. Since the impact forces are highly sensitive to the initial conditions (Gerritsen et al., 1995), the initial segment velocities were optimized with the control parameters to minimize the tracking error. Constraints on the segment velocities were enforced during the optimization that only allowed the velocities to vary within the range of those experimental values at ± 20 ms at touchdown.

The initial muscle activation levels for each simulation in the optimization search were determined by a two-step process. First, each muscle's excitation pattern was pre-integrated over the entire gait cycle using the first-order differential equation describing the activation dynamics (or excitation–contraction coupling) (Raasch et al., 1997). Second, the activation level at 100% of the gait cycle was then used as the initial activation level for that muscle since the activation level at 100% corresponds to the steady-state activation level at 0% of the gait cycle. The initial fiber velocity was set to zero for each simulation and the initial fiber and tendon lengths were determined by assuming static equilibrium between the fiber and tendon forces. Using the initial muscle activation level found above, the fiber and tendon lengths were found iteratively until muscle and tendon forces were equal. This force was used as the initial muscle force at $t = 0.0$.

2.6. Muscle-induced acceleration and segment power analysis

A segment power analysis was performed on the simulation data to quantify the flow of mechanical power generated by individual muscles (e.g. Fregly and Zajac, 1996). An individual muscle either generates (absorbs) mechanical power to (from) the legs, the trunk or both, or transfers power between the trunk and legs in either direction. These functions may also occur simultaneously (e.g. a muscle may transfer mechanical power between the legs and trunk while also generating power to the trunk or legs). A muscle can contribute to the power of a segment (i.e. accelerate a segment) it does not touch through the intersegmental reaction forces (e.g. Fregly and Zajac, 1996). The segments of interest were the trunk and left and right legs (contributions to the foot, shank, patella and thigh of each leg were summed and analyzed together). The net mechanical energy produced by a muscle over the gait cycle was computed by integrating the instantaneous muscle power (i.e. the product of the musculotendon force and velocity) over the gait cycle.

Each muscle's contribution to the instantaneous segment powers was determined at each instant in time from knowledge of the current state (generalized coordinates and velocities) of the system and the instantaneous accelerations induced by that muscle (Fregly and Zajac, 1996). The muscle-induced accelerations were determined by setting gravity and all velocities to zero, applying the one muscle force and its corresponding ground reaction force and center-of-pressure, and computing the resulting accelerations. The muscle's contribution to the ground reaction force and center-of-pressure was determined in a two-step process. First, the total ground reaction force and center-of-pressure was determined at time step i based upon the current state of the system. Then, at time step $i-1$, all muscle forces were applied to the system except for the muscle of interest and the equations-of-motion were integrated over the time step from $i-1$ to i ($dt = 0.0022$ s) and the ground reaction force and center-of-pressure was recomputed for the new state of the system. The muscle's contribution to the ground reaction force and center-of-pressure was determined as the difference in these quantities between the original and new system states. The process was then repeated for each muscle. The segment powers generated by each muscle were summed and compared to the corresponding musculotendon power to verify that they were equivalent. Since the right and left leg muscle coordination patterns were symmetrical, the data were analyzed only for the right leg muscles.

A muscle's contribution to support and forward progression was determined by quantifying its contribution to the acceleration of the trunk segment in the vertical and horizontal directions, respectively. This analysis was combined with the segment power analysis to identify the biomechanical mechanisms used by individual muscles to accelerate the trunk. Since a linear transformation exists between segment power and acceleration (Fregly and Zajac, 1996), the segment power analysis provides a clear interpretation of a muscle's influence on a segment. Positive power delivered by a muscle to a segment indicates that the muscle accelerated the segment in the direction of the movement; negative power indicates the muscle decelerated the segment. Segmental vertical power was defined as the time rate of change in its potential and vertical kinetic energy; horizontal power as the time rate of change in its horizontal kinetic energy. A muscle's contribution to swing initiation was determined by first quantifying the power delivered to the leg segments at each instant during pre-swing and then integrating over pre-swing to find the energy delivered to the leg (pre-swing = 50–60% gait cycle; Perry, 1992).

3. Results

A simulation was generated such that the simulated kinematics closely matched the group-averaged kinematics (Fig. 1), and the simulated kinetics (joint torques and powers; ground reaction forces) were near ± 2 SD of the experimental data (Fig. 2). Since the muscle excitation timing was constrained in the optimization, the muscle timing compared well with published EMG data (Fig. 3). Therefore, the timing of muscle force development throughout the gait cycle can be expected to represent normal human subject activity. The average simulation walking speed and stride time matched the experimental data (1.5 m/s and 1.1 s, respectively).

Both SOL and GAS provided trunk vertical support throughout single-leg stance and pre-swing (Fig. 4). Since the trunk is moving downward from mid single-leg stance through pre-swing as SOL and GAS act to accelerate the trunk upward, these muscles decelerate the trunk and cause trunk power in the vertical direction to be negative (Fig. 5: 30–55% gait cycle, dashed lines are negative).

In early single-leg stance (~ 10–25% gait cycle), both SOL and GAS slowed forward progression by decelerating the trunk forward, but GAS more so (Fig. 4); thus each reduces horizontal trunk power (Fig. 5, dotted lines negative; GAS > SOL). Since the trunk is moving upward then, and SOL and GAS provide trunk vertical support (i.e., their hip reaction force vectors have upward components), each causes vertical trunk power to increase (Fig. 5, dashed lines are positive). The net energetic effect on the trunk by SOL in this region is
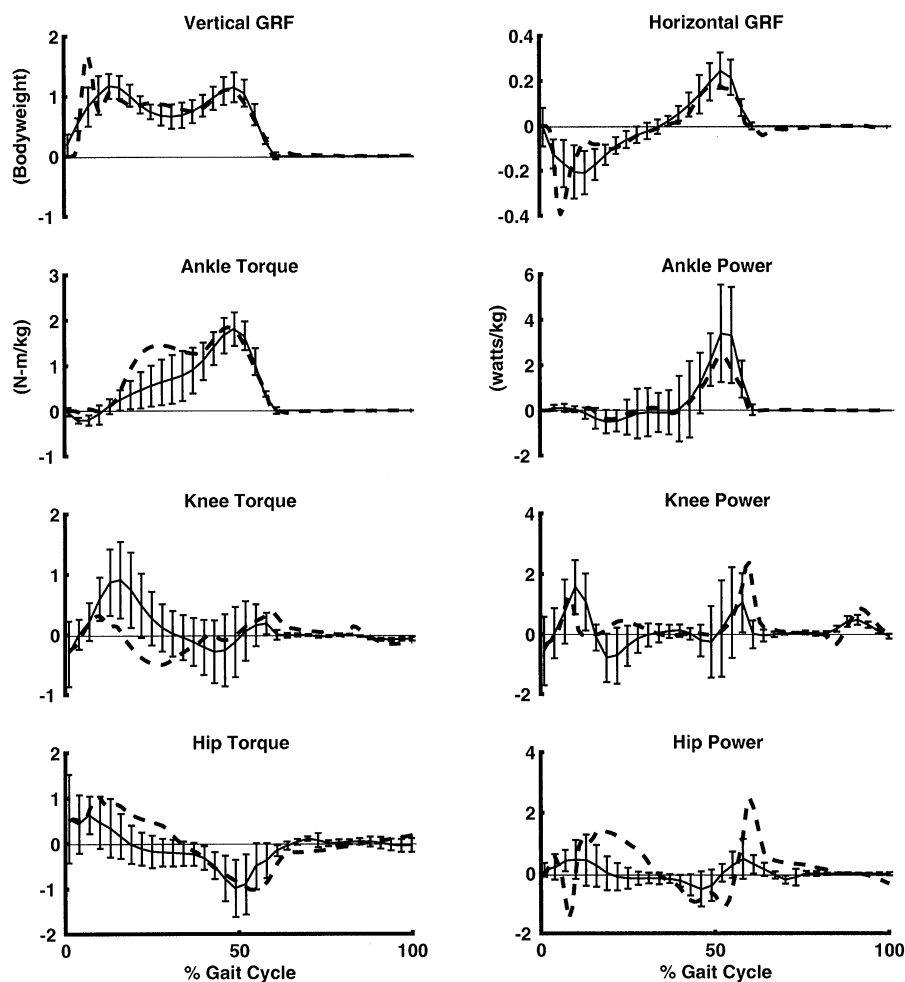
Fig. 2. Comparison of the simulation and group average experimental kinetic and kinematic data of the right leg during the gait cycle (right heel-strike to right heel-strike). All data were normalized by body mass, except the ground reaction forces were normalized to body weight. The experimental data are the average of the five subjects $\pm 2\,$SD.

close to zero (Fig. 5, SOL: area under solid line ≈ 0), whereas the net effect by GAS is to absorb trunk energy (Fig. 5, GAS: area under solid line is negative) because GAS decelerates the trunk horizontally more than SOL (Fig. 4) (i.e., the backward component of the hip reaction force vector caused by GAS is much greater than the component caused by SOL).

In mid single-leg stance (near 30% gait cycle), GAS still impedes forward progression, but only slightly (Fig. 4, GAS: dashed line is a little negative), whereas SOL now assists forward progression, but also only slightly (Fig. 4, SOL: solid line is a little positive). Although both SOL and GAS are near isometric (Fig. 6, SOL, GAS: solid lines ≈ 0), their muscle forces cause reaction forces in the leg and trunk enabling them to transfer much power between the leg and trunk, but in opposite directions (Fig. 6, SOL, GAS: dotted and dashed lines in each muscle are about opposite, and also opposite between SOL and GAS). SOL transfers power from the leg to the trunk; GAS

the opposite. The net effect of these reaction forces on the leg and trunk is to provide trunk and leg support, which ensures trunk and leg forward progression (see Discussion).

In late single-leg stance through pre-swing (40–60% gait cycle), GAS and SOL both provide forward progression (Fig. 4) and deliver power to the trunk (Fig. 6), but SOL much more so. Although excitation in both muscles has ceased by mid pre-swing, both muscles produce force throughout pre-swing because muscle deactivation (e.g., Ca^{2+} uptake by the sarcoplasmic reticulum) is not instantaneous. Since both muscles are shortening then, they produce positive power (Fig. 6, SOL, GAS: solid lines are positive). While the energy produced by SOL is delivered mostly to the trunk (Fig. 6, SOL: solid line $\approx$ dotted line), almost all the energy produced by GAS is delivered to the leg for swing initiation (Fig. 6, GAS: dashed line $\approx$ solid line) rather than to the trunk (Fig. 6, GAS: area under dotted line is small).
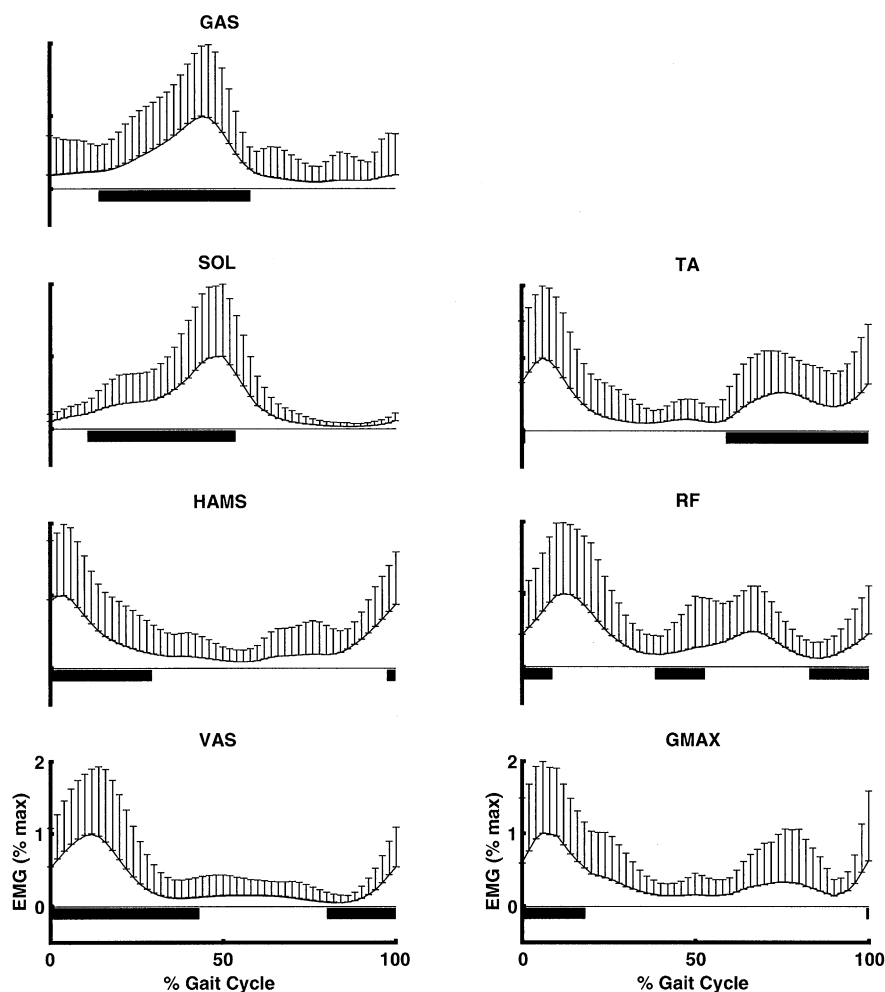
Fig. 3. Comparison of the simulation excitation timing with group average EMG data (from Winter, 1991) during the gait cycle. Black horizontal bars indicate simulation on–off excitation of the corresponding muscle. The EMG data is the group average + 1 SD. Onset and offset timing for BFsh (90% and 2%) and PSOAS (61% and 81%) are not shown (no EMG data).

4. Discussion

The objective of the present study was to quantify the contributions of the individual uniarticular and biarticular ankle plantar flexors to walking tasks of support, forward progression and swing initiation. Analyses performed on walking simulation data generated from a forward dynamics approach identified how the individual plantar flexors accelerate the trunk and leg and contribute to the power flow throughout the musculoskeletal system. Thus, how each muscle contributes to the three task goals was quantified.

We defined how each muscle contributes to support and forward progression by its ability to accelerate the trunk segment center-of-mass in the vertical and horizontal directions, respectively, rather than the whole body center-of-mass. This definition was used to facilitate direct comparisons with previous work (e.g. Hof et al., 1993; Kepple et al., 1997; Meinders et al., 1998) and was also suitable for our power analysis

framework that quantified the power flow between individual segments. In addition, since nearly 70% of the total body mass is located in the trunk segment, the trunk segment center-of-mass is both easily understandable and physically meaningful.

The musculoskeletal model and simulation were limited to the sagittal plane and only included those muscles that contribute primarily to sagittal plane motion. Since the majority of the mechanical work performed during locomotion is support against gravity and forward progression (e.g. Eng and Winter, 1995), both of which are sagittal plane functions, and the range of non-sagittal plane trunk rotations during normal walking is approximately $\pm 5°$ (e.g. Kadaba et al., 1990; Novacheck 1998; Stokes et al., 1989), this simplification was deemed justified.

The present musculoskeletal model and simulation framework have been used in a variety of pedaling studies to provide important insight into neuromotor control, joint loading and analysis techniques (e.g.
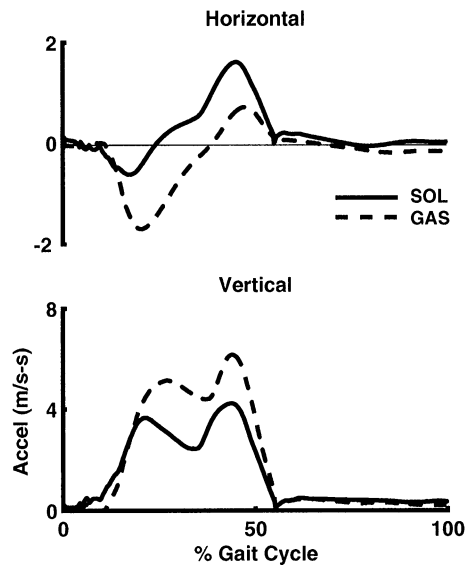
Fig. 4. Right-leg induced accelerations of the trunk in the horizontal (positive = forward) and vertical (positive = upwards) directions during the gait cycle by SOL and GAS.
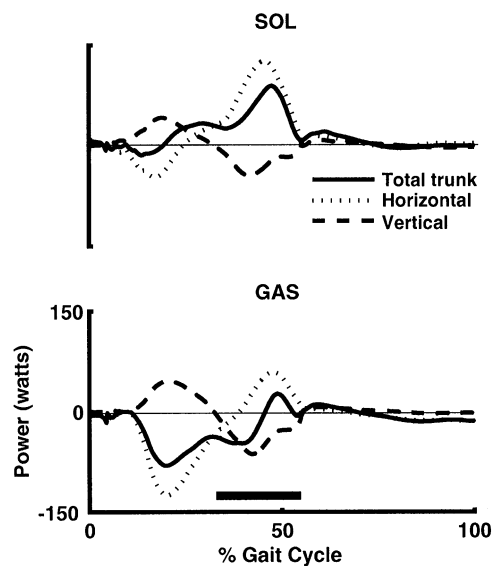

Fig. 5. Right-leg mechanical power to the trunk by SOL and GAS during the gait cycle. Horizontal power (*Horizontal*) is the time rate-of-change of the horizontal kinetic energy; vertical power (*Vertical*) is the time rate-of-change of the vertical kinetic and potential energy. Total power to or from the trunk (*Total trunk*) is the sum of the horizontal, vertical, and anterior/posterior tilting power (anterior/posterior tilting power is small and not shown). Horizontal bar indicates when the trunk is moving downward.
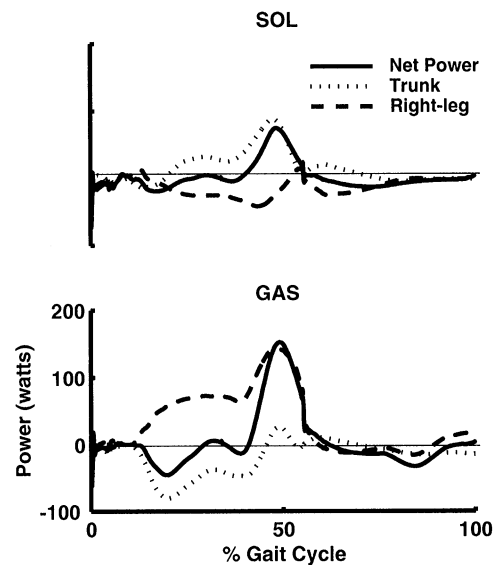

Fig. 6. Right-leg mechanical power produced by SOL and GAS and distribution to the leg and trunk during the gait cycle. The *net power* produced by SOL/GAS is the sum of the power to or from the leg segments (*Right-leg*), trunk segments (*Trunk*), and contralateral leg segments (which is small and not shown). Positive (negative) net power produced by the muscle indicates power generation (absorption). Positive (negative) power to the leg/trunk indicates the muscle is accelerating (decelerating) the leg/trunk in the direction of movement.

motoneuron pool (including sensory feedback). Therefore, the walking patterns were not assured to be at steady-state and as a result might be sensitive to the initial conditions. To assess this sensitivity, we examined the walking speed of the model throughout the gait cycle and found the deviation from the experimental data to always be within $\pm 5\%$. In addition, we examined the mechanical energy of the trunk segment and found the initial and final values to also be within $\pm 5\%$ of each other. In addition, other studies using similar musculoskeletal models have found their results to be insensitive to reasonable changes in various model parameters including activation and deactivation time constants (Piazza and Delp, 1996; Raasch et al., 1997), subject height (Schutte et al., 1993), maximum isometric force (Neptune and Hull, 1998) and lower extremity inertial properties (Piazza and Delp, 1996).

The simulation reproduced the salient features of normal walking mechanics. The most notable discrepancy between the simulation and the experimental data occurred in the hip joint power because the model required the orientation of the trunk to be controlled by a limited number of muscles in the legs (cf., muscles that attach to the pelvis and trunk). The lack of control allowed greater than normal trunk oscillations to occur, especially at impact. However, this discrepancy at the hip joint was not deemed critical in our interpretation of individual ankle plantar flexor function. The muscle excitation timing matched well with experimental EMG

Neptune and Kautz, 2000; Neptune et al., 2000a; Neptune and van den Bogert, 1998). But in contrast to pedaling, steady-state walking simulations without sensory feedback are difficult to achieve (e.g. Gerritsen, 1997). In our model, the muscle excitations function as open-loop controls without modification by sensory feedback, although we assume that the control signal represents a summation of all influences on the

patterns even though much latitude existed (±25% of average EMG timing), and the magnitudes of SOL and GAS were characterized by increasing values prior to toe-off, which also agrees with EMG data (e.g. Winter, 1991, Perry, 1992), even though no constraints were placed on the magnitudes. Of particular interest were the ankle-joint torque and power, and horizontal and vertical ground reaction force profiles that have been used to interpret the plantar flexor group function throughout the literature (e.g. Perry, 1992; Winter, 1991). The simulation replicated these measured patterns almost always within ±2 SD. Therefore, we have confidence that the simulation can be further analyzed to identify muscle function.

The contribution of individual muscles to the ground reaction force and center-of-pressure had to be quantified in order to determine the net contribution of individual muscles to the acceleration and power of the leg and trunk segments. The foot-ground contact model used in the present study utilized 30 stiff visco-elastic elements that store potential energy in the spring elements from all the forces acting on the system. Since the spring elements are relatively stiff and non-viscous relative to the total musculoskeletal system, stored energy is released quickly and energy dissipation small. To decompose the ground reaction force and center-of-pressure into the contributions of each muscle, we integrated the equations-of-motion without applying the corresponding muscle force to identify how it influenced these quantities. We performed a sensitivity analysis on the step size to see how it would affect our interpretation of muscle function. The segment power analysis, performed with different integration time steps ($dt = 0.0011$ s to $dt = 0.022$ s), revealed that the qualitative interpretation of muscle function was generally insensitive within the range (0.0022 s $< dt < 0.011$ s), although minor differences were apparent quantitatively (i.e., the functional role of the muscle was robust with respect to the integration step size). At step sizes too small, there was not enough time for changes in the ground reaction force to develop. At step sizes too large, the system dynamics were dramatically altered which caused the ground reaction force to become inconsistent with the movement. Therefore, we chose a step size within the insensitive range ($dt = 0.0022$ s). As a check, we compared the musculotendon power with the summed segment powers produced from the muscle induced accelerations and found that at no point in the gait cycle was the difference greater than 0.5%. Thus, the mechanical energy of the system was conserved in the analysis.

It should be noted that the "functional role" of each muscle was also robust with respect to the excitation magnitude and muscle strength since how each muscle is able to accelerate the trunk or leg segments at each instant in the gait cycle is entirely determined by the model configuration. Therefore, these parameters mainly affect the magnitude of the contribution to support, progression or swing initiation.

The simulation results revealed that SOL and GAS each shorten to generate nearly all the positive work of ipsilateral muscles during late single-leg stance through pre-swing (~ 40–60% gait cycle; power of other muscles are not shown in Fig. 6 but were computed). This result is consistent with suggestions from previous studies examining net ankle joint power (e.g. Robertson and Winter, 1980; Winter, 1983; Meinders et al., 1998). In agreement with hypotheses that the plantar flexor group provides an active push-off in this region of the gait cycle (Winter 1983; Kepple et al., 1997), we found that the contribution of SOL and GAS to support and forward progression (Fig. 4) dominate the contributions of the other muscles (Fig. 7, 40–60% gait cycle).

However, nearly all the energy produced by GAS during late single-leg stance through pre-swing is delivered to the leg (Fig. 6, GAS), whereas SOL generates all its energy to the trunk (Fig. 6, SOL) to provide forward progression and support (Fig. 5). These different functions of SOL and GAS were not revealed, nor could they be, with net joint moment analyses (Winter 1983; Kepple et al., 1997). The production of substantial energy by GAS in pre-swing and its delivery to the leg is consistent with the net role of the combined plantar flexors being to initiate swing (Hof et al., 1993; Meinders et al., 1998) because GAS delivered more
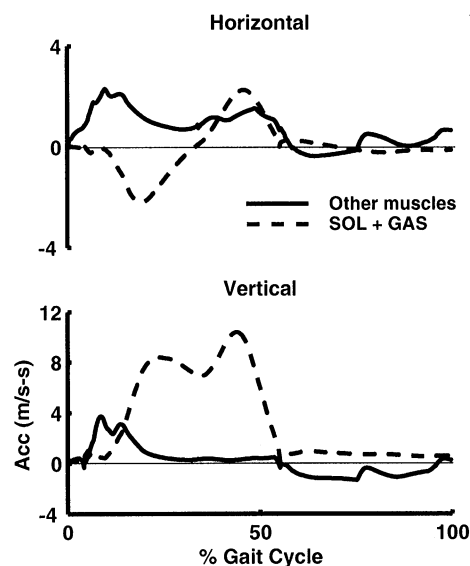

Fig. 7. Induced trunk horizontal and vertical accelerations by the right-leg SOL and GAS compared to all other right-leg muscles. Forward progression (horizontal acceleration) is provided during early stance into single-leg stance by the other muscles (*Other muscles*), which is comparable to the progression provided by SOL and GAS during late single-leg stance through pre-swing (SOL+GAS). The majority of support occurs during single-leg stance through pre-swing from SOL and GAS.

energy to the leg than SOL delivered to the trunk then (Fig. 6, compare area under solid lines). Although, the data is not presented in detail here, GAS was not the only contributor to swing initiation. The inactive uniarticular hip flexors and contralateral active biarticular hamstring muscles also contributed to increasing the energy level of the leg during pre-swing.

In contrast to previous studies (e.g. Kepple et al., 1997; Winter, 1983), the plantar flexors were found not to be the only major contributors to forward progression over the gait cycle (Fig. 7). Other muscles contribute significantly to progression throughout stance (Fig. 7). These important contributions from other muscles were not found by Kepple et al. (1997) in their induced acceleration analysis using net joint moments because they did not study the region where the other muscles contribute the most, which is where the ground reaction force is directed posteriorly (Fig. 1, ~0–25% gait cycle). The other muscles' contributions were not found by Winter (1983) because net joint powers cannot be uniquely decomposed into individual muscle contributions, nor can inverse dynamics analyses be used to determine individual muscle contributions to the acceleration of each segment (Zajac, 1993).

In early single-leg stance, when the ground reaction force is still directed posteriorly after double-leg stance (~10–25% gait cycle), both SOL and GAS increasingly provide support for the trunk (Fig. 4) as the other muscles decrease in theirs (Fig. 7, Vertical: compare the dashed line with the solid line). The trunk support by each of the plantar flexors during this region is, however, at the expense of the forward trunk deceleration caused by these muscles (Fig. 7, Horizontal: dashed line is negative 10–35% gait cycle) due to their induced posteriorly directed hip joint reaction force. However, during the rest of stance, SOL and GAS together do provide forward progression (Fig. 7, Horizontal: 35–60% gait cycle) as they dominant the support the trunk (Fig. 7, vertical: 15–60% gait cycle), which is in agreement with Kepple et al. (1997).

Although previous studies have suggested that the plantar flexors function to provide lower leg stability in mid single-leg stance by decelerating forward rotation of the tibia so the knee accelerates into extension (Simon et al., 1978; Sutherland et al., 1980) as a part of the controlled roll-off theory (Perry, 1992), our simulation data revealed, however, SOL, not GAS, performs this function. (Fig. 8, near 30% gait cycle). In contrast, GAS acted to accelerate the knee into flexion then (Fig. 8, near 30% gait cycle). VAS was the primary contributor to knee stability during early stance into single-leg stance while RF was the primary contributor at the end of single-leg stance. But SOL was the only muscle to provide this stability throughout single-leg stance. Therefore, impaired SOL activity would necessitate a compensatory mechanism to prevent collapse of the
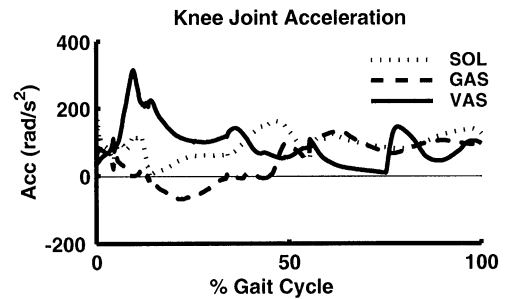

Fig. 8. Knee joint angular accelerations induced by SOL, GAS and VAS. VAS accelerates the knee into extension (positive acceleration) during early stance into single-leg stance. Then SOL accelerates the knee into extension by decelerating the forward progression of the shank during single-leg stance through pre-swing. GAS mostly accelerates the knee into flexion in single leg stance.

knee during the middle of single-leg stance. The most likely mechanism would be prolonged VAS activity which is in agreement with clinical observations (e.g. Murray et al., 1978; Sutherland et al., 1980).

However, our results do not support the controlled roll-off theory for forward progression in late single-leg stance and pre-swing since both SOL and GAS accelerate the trunk forward then (Fig. 7). Perry (1992) suggests that the second burst in the ground reaction force is from a passive mechanism rather than the ankle plantar flexors contributing directly to forward progression. In contrast, our results show that the SOL and GAS provide 60% and 25%, respectively, of the trunk forward acceleration during the second burst of the ground reaction force (40–50% gait cycle).

We believe the action of SOL to slow tibial rotation and provide knee stability during single-leg stance (near 30% gait cycle) is part of an overall synergistic and efficient mechanism of SOL and GAS to provide support and maintenance of forward progression of both the trunk and leg. Although SOL and GAS do not produce energy in this region of the gait cycle because they are isometric, they each have *different* energetic effects on the trunk and legs that allows them *together* to effectively transfer energy between the leg and trunk. Their combined reaction force at the hip, and their isometric activity, allows for the efficient interchange of trunk potential and kinetic energy as the trunk rises and falls around its apogee, consistent with the proposed ballistic motion of the body in single-leg stance (Mochon and McMahon, 1980). Their combined reaction force on the leg segments similarly provides for efficient potential and kinetic energy exchanges among them as the leg rises and falls that allows the energy state of the leg to remain unchanged. By supporting both the trunk and leg while isometric before and after apogee of the body, SOL and GAS synergistically provide for efficient forward progression as well. Finally, no other stance leg muscles are active in this region of the cycle to provide this function.

In summary, both SOL and GAS provide vertical support throughout single-leg stance. During mid single-leg stance, SOL and GAS have opposite energetic effects on the leg and trunk that together ensures support and forward progression of both the leg and trunk. During pre-swing, only GAS contributes to swing initiation. These results illustrate why the loss or impairment of force generation by either SOL or GAS would clearly impact walking performance (e.g. Mueller et al., 1995; Nadeau et al., 1999; Winter et al., 1990). However, the results of this study also illustrated that other muscles contribute significantly to forward progression (Fig. 7) and further study is needed to understand the synergistic interactions between the plantar flexors and other muscle groups during normal walking.

Acknowledgements

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